



Courtship diverges with foraging behaviour in artificially selected populations

Gemma L. Cole^{*}, John A. Endler

Centre for Integrative Ecology, School of Life and Environmental Science, Deakin University, Waurn Ponds, VA, Australia

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The sensory drive hypothesis proposes that natural selection on certain behaviours will alter sensory system properties and result in correlated evolution of unrelated behaviours reliant on that sensory system. Here, we used artificially selected populations to demonstrate that selection on colour-based foraging behaviour is associated with divergence of male sexual display behaviour. In a previous experiment, populations of guppies, *Poecilia reticulata*, were selected for increased chase behaviour towards a red or a blue prey item. In this study, we conducted behavioural trials using these artificially selected populations to show that male mating behaviour diverged after artificial selection on foraging behaviour. The behavioural trials showed that the number of courtship displays and total mating activity were reduced in populations selected to chase a red prey item compared to control populations and populations selected to chase a blue prey item. These results show that artificial selection for a given behaviour can result in changes in unrelated behaviours. Our study has shown that selection on a nonmating behaviour may have consequences for sexual behaviour and the evolution of sexual signalling that has previously not been considered.

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The complex nature of behavioural traits means that the evolution of one behaviour often results in the evolution of other, seemingly unrelated behaviours. This can be due to a number of factors such as pleiotropy (Anholt & Mackay, 2004), simultaneous responses to environmental change (Candolin, 2009), linked functions and sensory drive (Endler & Basolo, 1998; Endler, 1992; Ryan, 1990). The sensory drive hypothesis (Endler, 1992) proposes that natural selection on certain behaviours will alter sensory system properties and result in correlated evolution of behaviours reliant on that sensory system. For example, environmentally induced changes in the visual system (Kranz, Forgan, Cole, & Endler, 2018b) have been shown to influence visually based behaviours such as sexual signalling (Cole & Endler, 2016; Kranz, Cole, Singh, & Endler, 2018a), mate choice (Cole & Endler, 2015b; Fuller & Noa, 2010) and foraging behaviour (Cole & Endler, 2015a; Fuller, Noa, & Strellner, 2010) independently. However, selection on one behaviour may result in the evolution of another if both behaviours are mediated by the same sensory or decision-making processes.

A number of studies have shown that unrelated behaviours sharing a common sensory system have the potential to coevolve.

For example, water mites, *Neumania papillator*, use vibratory cues to detect both prey and mates (Proctor, 1991), and the visual physiology of guppies, *Poecilia reticulata*, is thought to link mate preferences (Sandkam, Young, & Breden, 2015) and foraging behaviour (Rodd, Hughes, Grether, & Baril, 2002). If selection is applied to a sensory system, either directly or indirectly, it is possible that behaviours reliant on that system will evolve (Cole, 2013). For example, it has been shown that visual sensitivity responds to selection (Grether, Hudon, & Endler, 2001) and that changes in vision have the potential to influence behaviour (Melin, Fedigan, Hiramatsu, Sendall, & Kawamura, 2007; Sandkam et al., 2015). Two unrelated behaviours that frequently rely on the same senses are foraging and reproductive behaviours. These behaviours provide an opportunity to test whether selection on one behaviour results in the coevolution of the other. If selection on one of these behaviours alters the physiological processes that underpin the other, we would expect to see associated changes in the two behaviours.

Artificially selected populations allow us to test the correlated evolution of traits and behaviours. In a previous experiment investigating sensory drive, artificial selection was performed on guppies for increased foraging behaviour towards either red or blue prey items, with the intention of inducing indirect selection on

^{*} Correspondence: G. L. Cole, Centre for Integrative Ecology, School of Life and Environmental Science, Deakin University, Waurn Ponds, 3216, Victoria, Australia.
E-mail address: gemma.cole@deakin.edu.au (G. L. Cole).

colour-based preferences via visual or decision-making systems (Cole & Endler, 2015a). Fish were required to chase either a red or a blue spot produced by a laser on the bottom of a tank. They were selected on the basis of a chase score that consisted of the number of chases towards the spot, the number of orientations towards the spot and the latency to perform either of these actions. Individuals with the highest chase score were selected. Cole and Endler (2015a) reported a response to artificial selection for chase behaviour in the lines selected to chase red prey items but no response in chase behaviour in the lines selected to chase blue prey items. Although a response in the blue-selected lines was not found for chase behaviour, we did find a response in the blue-selected lines for the ratio of fish that responded to the spot (by either orienting or chasing) to the number of fish that did not respond to the blue spot (Appendix Table A1).

Following selection, fish were tested for chase behaviour towards coloured laser spots for which they were not selected, to identify differences in more general colour-based preferences between the selection lines (Cole & Endler, 2015a). Evidence was found that suggested that the fish in the selected lines diverged in visual perception and/or colour-based decision-making processes: both sexes changed their behaviour towards the colours to which they were naïve. Compared to control lines, blue-selected lines reduced chase responses when tested with a green and a red laser spot, while red-selected lines reduced chase responses to a green and a blue laser spot. If colour vision and/or associated decision-making processes were selected indirectly, it is possible that other behaviours reliant on these processes may diverge between the selected lines.

Behaviours that may be affected by visual perception and/or decision-making processes include foraging behaviours, mate choice behaviours and courtship behaviour. The male sexual signal and female mate preferences of the populations used in this study have diverged between selected lines (Cole & Endler, 2018). Here, we investigated potential effects of the artificial selection on male courtship behaviours. Male guppies have distinct courtship behaviours that can be divided into two categories: sigmoid displays, where males curve their bodies into an S-shape and jerk backwards and forwards in front of the female, and sneaky copulation attempts, where the males attempt to inseminate the female non-consensually (Houde, 1997). These behaviours, particularly courtship displays, are important in facilitating female mate choice (Houde, 1997; Kodric-Brown & Nicoletto, 2001). If artificial selection on foraging behaviour has affected visual or cognitive processes (the assimilation and subsequent processing of information received from sensory functions), we would expect to see differences in sexual behaviour between the artificially selected lines. This in turn could lead to different directions of sexual selection. Here, we tested the hypothesis that artificial selection on foraging behaviour will be associated with changes in male courtship behaviour. The red-selected populations showed a strong response to artificial selection compared to the blue-selected and control populations. We therefore predicted that male mating behaviours will diverge in a similar manner. More specifically, because we selected for an increase in movement behaviour in the red-selected lines, we predicted that males in these lines will increase the number and duration of courtship behaviours compared to the blue-selected and control lines.

METHODS

Husbandry

Guppies used for the initial selection experiment were first- to second-generation wild-caught fish from Alligator Creek,

Queensland, Australia (19°26.79'S, 146°58.65'E). Fish were maintained at $24 \pm 1^\circ\text{C}$ and a 12:12 h light:dark regime with brown and green flake food provided daily. Individuals were housed in large 194-litre glass tanks containing around 150 juveniles and adults of both sexes (sex ratio ca. 1:1) prior to use in the experiments.

Artificial Selection for Colour-based Foraging Behaviour

This study builds upon a previous study in which male and female guppies were artificially selected for chase behaviour towards red and blue prey items (Cole & Endler, 2015a). Here we analysed male sexual behaviour in those populations. For the artificial selection methods see Cole and Endler (2015a) and the Appendix. Briefly, a proxy for coloured prey items was created in the form of 3 mm diameter projected spots moving on a gravel background, which the fish could chase. Populations of fish were selected for increased chase behaviour towards red spots (R1, R2) or blue spots (B1, B2), with two controls not subject to selection (C1, C2). The selection criteria combined three behaviours into a chase score: latency to chase the spot, number of orientations towards the spot and number of chases towards the moving spot. Artificial selection for increased chase behaviour was conducted over four generations on both males and females, stopping at generation 4. Cole and Endler (2015a) showed that colour chase preferences in these selected populations are heritable: a positive response to selection was observed for chase score in both of the red-selected lines, but only one (R1) was significantly different from zero. No response for chase behaviour was observed in the blue-selected lines. Although we do not have direct evidence for changes in the sensory system, the response to colours for which the fish were not selected (blue-selected lines reduced chase responses to green and red, while red-selected lines reduced chase responses to green and blue) suggests that changes in visual processing or colour-based decision making may have occurred in both the red- and blue-selected lines (Dowling, 2012).

Courtship Activity Trials

We recorded mating activity (courtship displays and sneak copulation attempts) of males from each selected line to test whether artificial selection for foraging behaviour had influenced mating behaviour. We randomly selected 27 males from each of the selected lines. Each male was placed into a 6-litre tank with a group of three females. Nine female groups were used, with each being seen by three males. Females were selected quasirandomly from stock (unselected) populations so that none looked obviously gravid and all were size-matched to within 3 mm. None of the females gave birth during the trial period. This is important because it shows that all females were in a similar state of receptivity throughout the experiment (Liley, 1966). Also, none of the females showed aggression towards the males or erratic behaviour which would bias the results. Test males were removed from their home tanks and isolated for 24 h prior to the trials commencing to standardize motivation.

After a 2 min acclimation period, the number of courtships, the number of sneak copulation attempts and the total mating activity (the number of courtship displays plus sneak copulation attempts) of the males was recorded. Trials ran for 15 min each. Males were returned to their home tank at the end of the trial. Trials were conducted at the same times each day over a 6-day period: one selected population replicate per day in a random order. Four males were excluded from the results due to illness. Final sample sizes were as follows: C1=26, C2=26, B1=25, B2=27, R1=26, R2=27 (total males=157). No copulations were observed during any of the trials.

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